

PATTERNS OF STROMATOPOROID GROWTH IN LEVEL-BOTTOM ENVIRONMENTS

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ABSTRACT. Stromatoporoids in argillaceous level-bottom limestones of the Upper Visby Beds in the Silurian of Gotland, Sweden, show a variety of features of growth form, within a spectrum of coenosteal shapes from laminar through low to high domical. Many coenostea show interdigitations of sediment in their margins, attributable to intermittent sedimentation, while others show abrupt changes in growth direction, which are the results of movement, often leading to overturning. Stromatoporoids frequently survived these agents and continued to grow, often resulting in different morphotypes from those which would have been produced in the absence of sedimentation and movement; serious problems of shape identification and shape classification exist as a consequence. Variations in the effects of sedimentation and movement are recognizable in the specimens studied and the stromatoporoids therefore record a variety of events occurring at the sea bed during their lives. The four most abundant stromatoporoid species in the Upper Visby Beds show variations in morphology. *Densastroma pexisum* Yavorsky is commonest and in general has a taller shape than *Clathrodictyon simplex* Nestor, *Pseudolabechia hesslandi* Mori, and *Stromatopora impexa* Nestor. The reasons for such variations are unclear but may be related to a number of factors such as sedimentation, current activity, substrate consistency, or availability of food and oxygen.

STROMATOPOROIDS exist as a wide range of growth forms and the difficulties involved in dividing this range into recognizable groups of shapes are reflected in the small amount of literature containing useful information on stromatoporoid morphotypes (e.g. Broadhurst 1966; Abbott 1973; Kapp 1974; Cornet 1975; Kobluk 1975; Kershaw and Riding 1978, 1980). The majority of stromatoporoids have a common plan of accretionary growth by successive layers (laminae) leading to the familiar range of laminar, domical, and bulbous forms which can be expressed as a geometrical array (Kershaw and Riding 1978). Dendroid stromatoporoids form a distinct group and are not considered here.

Laminar, domical, and bulbous forms are most easily recognizable when the stromatoporoids grew on a flat substrate and were not subjected to sedimentation or dislocation so that their shapes are preserved as being clearly laminar, domical, or bulbous. However, stromatoporoids are relatively shallow-water benthic organisms and as such were exposed to dynamic factors of the environment, such as sedimentation and turbulence. Problems arise in classifying the shape of a particular individual which preserves the effects of these factors. A domical coenosteum which was overturned but continued to grow from undamaged surfaces developed an overall shape which is no longer domical, but was nevertheless created by a domical style of growth. This is also true for coenostea which have suffered frequent sedimentation, leaving them with ragged margins and an exaggerated vertical dimension. The problem is further compounded by inherent irregularity of many growth forms, particularly in Devonian carbonate complexes (e.g. Fischbuch 1968; Noble 1970; Cornet 1975) where a number of different types of mamelons and irregular protrusions can complicate the shape of a coenosteum. Various combinations of these factors can lead to an individual which is not immediately recognizable as belonging to a particular group of shapes in the Kershaw and Riding (1978) scheme. The problems involved in analysing the biological processes which determined the shapes are thus greatly increased.

These problems are of course a reflection of the growth and development of coenostea but a further consideration has a powerful influence on morphological groupings of stromatoporoids: the plane of section. Stromatoporoids, especially reef-building forms, are usually seen in vertical section in cliff

faces and drill cores and the practice of shape classification is mostly carried out on two-dimensional sections. Thus we are trying to classify three-dimensional shapes from two-dimensional views. Serial sectioning would allow the three-dimensional form of a stromatoporoid to be characterized but this is not practicable in most situations and we are, therefore, simply stuck with the problem. Plane of section is not a severe difficulty in stromatoporoid-bearing rocks where coenostea are preserved upright and lack the effects of changing growth direction (see Kershaw and Riding 1980), but forms which have been overturned and contain several episodes of growth in different directions present serious problems of classification based on a single plane of section.

In a typical assemblage of stromatoporoids there is a mixture of growth forms: (a) those which grew as regular laminar, domical, or bulbous forms and have not been disturbed during their lives; (b) those which began growth in such a way but subsequently were affected by dynamic environmental factors which produced effects attributable to movement and sedimentation; and (c) forms with inherent growth irregularities which may or may not include the effects of b. An example of such an assemblage is found in the Upper Visby Beds on Gotland, Sweden. This contains very few forms of category c. The assemblage usefully illustrates the problems outlined above and the means by which some of them can be filtered out so that the factors controlling the basic morphologies may be more clearly identified. The relationships between genotype and morphotype of the stromatoporoids can then be more easily examined. Cornet (1975) and Kershaw (1981) have already demonstrated that an

EXPLANATION OF PLATE 20

Stromatoporoids from the Upper Visby Beds showing effects of sedimentation and movement described in the text. All figures are vertical sections. Some material is deposited in the British Museum (Natural History) (prefix BM(NH); the remainder (prefix SGU) with the Swedish Geological Survey.

Fig. 1. Smooth enveloping domical coenosteum of *Denastroma pexisum*. Note that (a) the specimen is composed initially of two coenostea which merged as they grew, and (b) no sedimentation events are recorded in the specimen. Korpklint 1, $\times 0.6$. SGU Type 1439.

Fig. 2. Upper coenosteum: smooth non-enveloping low domical form of *D. pexisum* showing *Trypanites* borings in the upper surface. Lower coenosteum (below line): low domical ragged form of *Stromatopora impeya* showing small sedimentation events interrupting growth at regular intervals. A small heliolitid colony (centre) grew on the upper surface before the *D. pexisum* covered it. Ireviken 3, $\times 1$. BM(NH) H 5442.

Fig. 3. Domical coenosteum of *D. pexisum* (on coral debris) showing damage at the right-hand flank, the damaged area being encrusted by a laminar coenosteum of *Clathrodictyon simplex*. The latter extends underneath the *D. pexisum* suggesting that at one time the right edge was uppermost. Ireviken 3, $\times 1.25$. SGU Type 1440.

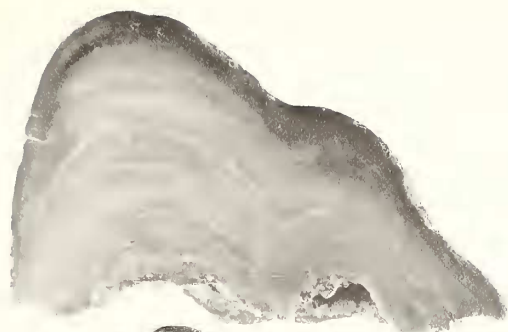
Fig. 4. Part of a coenosteum of *D. pexisum* (lower) encrusted by a bryozoan (thin white layer), in turn encrusted by a low domical smooth, non-enveloping form of *C. simplex*. Häftingsklint 1, $\times 1.25$. SGU Type 1441.

Fig. 5. Domical coenosteum of *D. pexisum* showing how movement has generated a bulbous outline. The right-hand coenosteum grew first and was then turned so that its left-hand edge was uppermost (with some damage to the fragile marginal areas on the left) and continued growth to produce a new coenosteum on the left of the photograph. Ireviken 3, $\times 0.8$. SGU Type 1442.

Fig. 6. Complex intergrowth of laminar and domical forms of *C. simplex* and alveolitid tabulates with intermittent sedimentation. The complex developed on a stable base of a halysitid colony (below line). Ireviken 3, $\times 1$. SGU Type 1443.

Fig. 7. Complex specimen showing development of ragged coenostea followed by overturning and regrowth. Specimen contains mostly *D. pexisum* but small coenostea of *C. simplex* and *S. impeya* are involved. Ireviken 3, $\times 0.6$. SGU Type 1444.

Fig. 8. Composite specimen of *D. pexisum*, *C. simplex*, and alveolitid tabulates to produce a structure with at least nine growth phases. It is clear that the specimen was overturned many times. Ireviken 3, $\times 0.6$. SGU Type 1445.



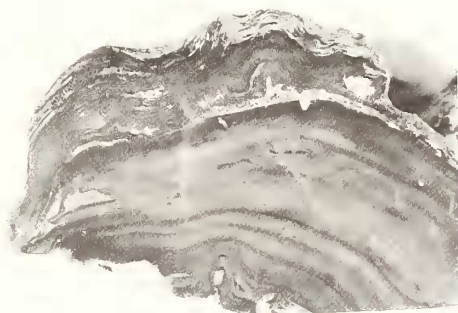
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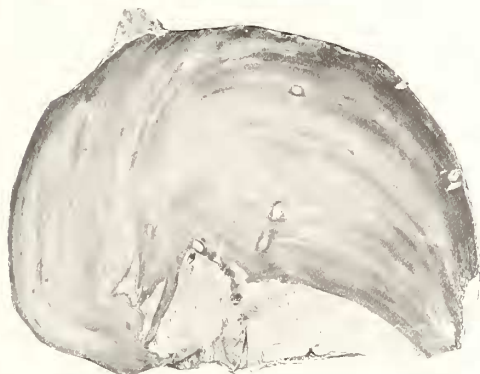
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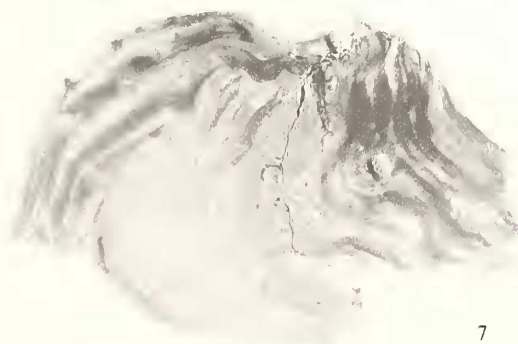
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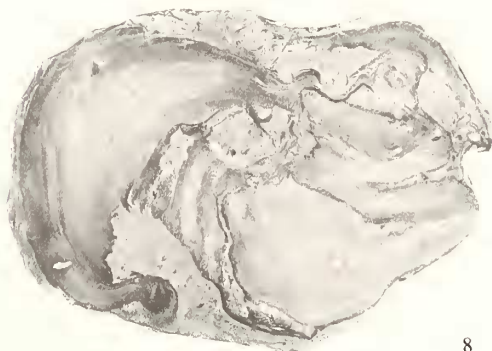
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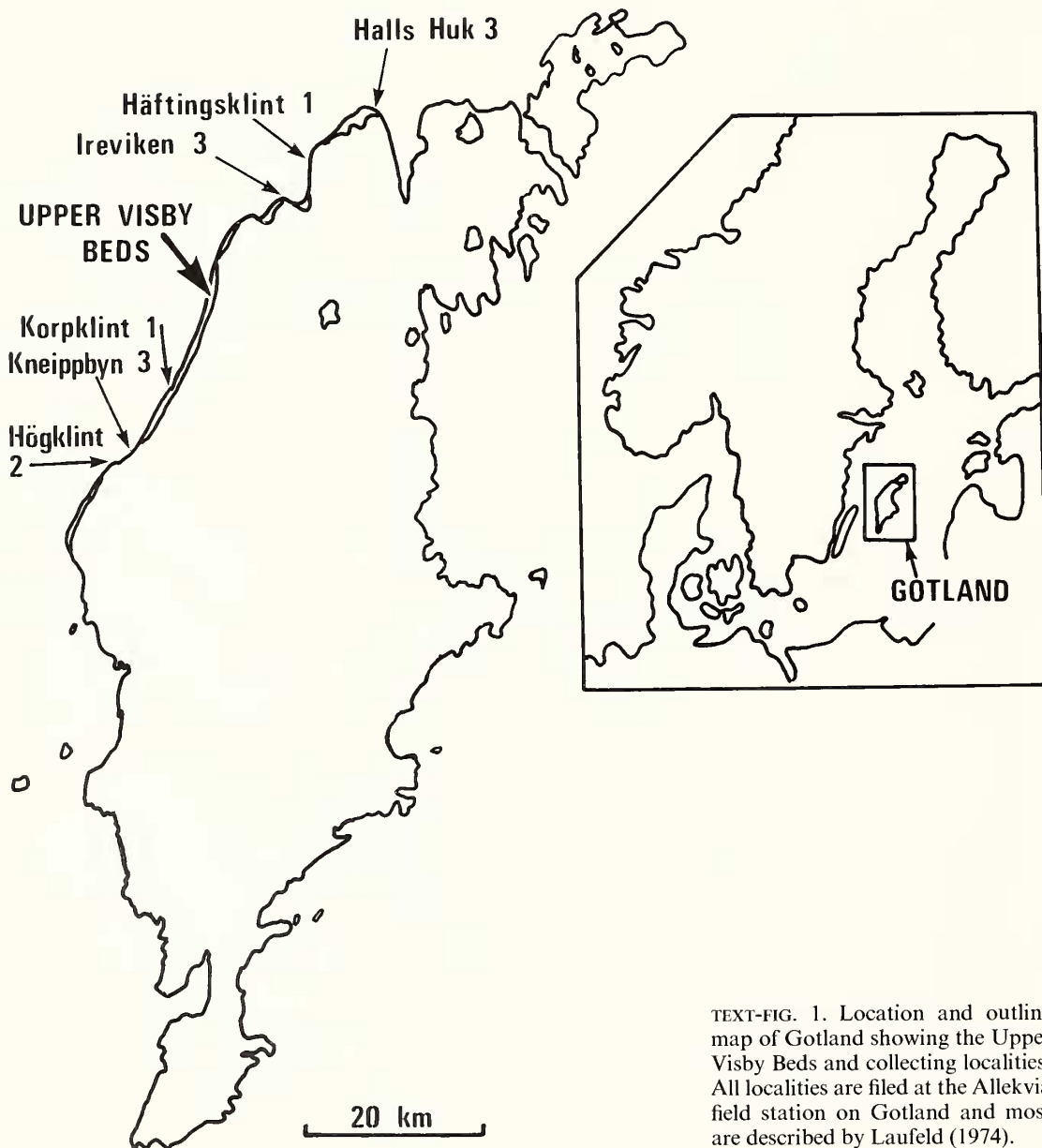
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understanding of stromatoporoids as organisms needs a conjunctive shape-species study: the Upper Visby Beds contain a small suite of species and the range of shapes of each is considered here.

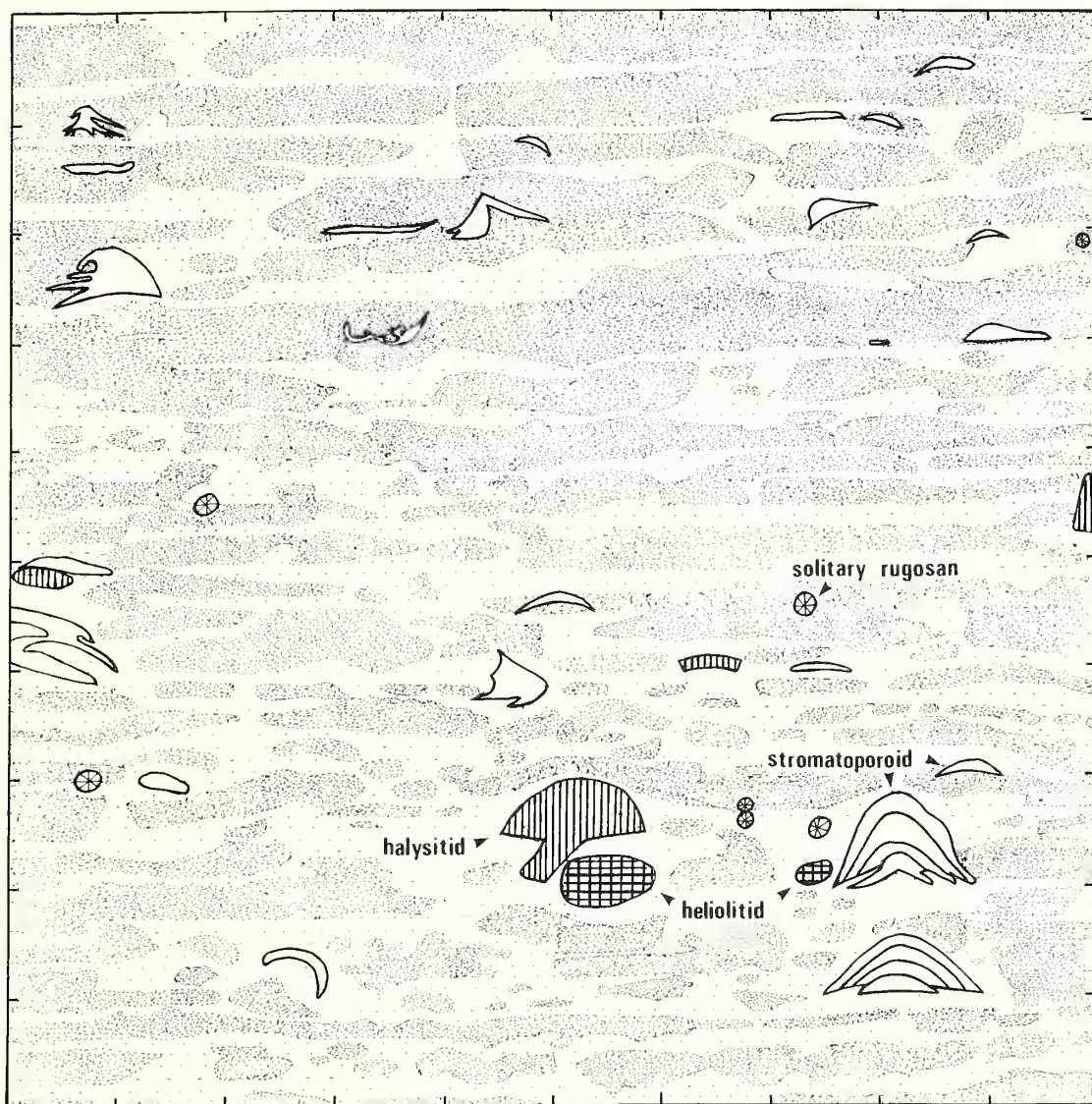
Importantly, stromatoporoids from the Upper Visby Beds can be easily extracted from the friable sediment; thus unlike rock sections where complete specimens are not normally obtainable, the three-dimensional structure of the Upper Visby specimens can be studied. Because of the availability of entire specimens, an adequate description of the history of growth or any coenosteum from these beds can be obtained by examination of a single (usually vertical) section through it, together with observations of its surface features.



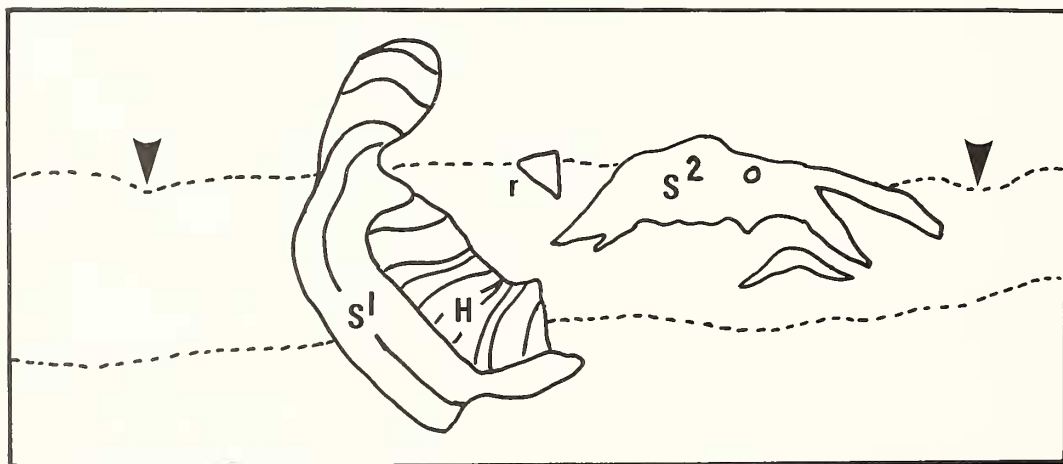
TEXT-FIG. 1. Location and outline map of Gotland showing the Upper Visby Beds and collecting localities. All localities are filed at the Allekvia field station on Gotland and most are described by Laufeld (1974).

THE UPPER VISBY BEDS

The Upper Visby Beds of Hede (1960) are dated as earliest Wenlock (see Jaanusson *et al.* 1979) and occur as a series of outcrops of maximum thickness 15 m, along the north-west coast of Gotland approximately following the strike of the beds (text-fig. 1). Dips are very low but there are local low amplitude folds due largely to the deformation of these incompetent beds by the weight of the overlying Högklint reefs (Eriksson and Laufeld 1978). Fossil contents are very variable and this is reflected by the occurrence of the stromatoporoids. The Upper Visby Beds are composed largely of alternating bands of mudstones and wackestones, much of the sediment being poorly consolidated.



TEXT-FIG. 2. Detailed map of 1 sq. m of vertical section of the Upper Visby Beds at Halls Huk 3 showing positions and attitudes of stromatoporoids and corals. Note the low faunal density. Heavy stipple: incomplete argillaceous limestone bands; light stipple: shale.



TEXT-FIG. 3A and B. Band of coarse debris (centre, arrowed) in fine-grained strata. Stromatoporoid (S1) overgrew a halysitid (H); the composite was overturned and S1 shows continued upward growth. Stromatoporoid S2 is preserved upright. r is a rugosan. Halls Huk 3, $\times 0.5$.

They form part of a shallowing-up sequence which begins with the underlying Lower Visby Beds (mostly unfossiliferous muds with little calcareous content), passes through the Upper Visby Beds, and ends with the Höglint and Tofta Beds (a complex mosaic of facies comprising reefs, inter-reef muds, and crinoidal grainstones as the main components). The Upper Visby Beds show a gradual upward increase in calcareous content and faunal diversity, but as a whole represent a relatively deep, generally quiet environment with a low diversity fauna. Accordingly the beds lack evidence of cross-bedding, scouring, or channelling by currents but indications of periodic disturbance (Jaanusson *et al.* 1979), particularly towards the upper parts, are present as packstone bands of skeletal debris which include not only shell material, but also stromatoporoid and coral coenostea (text-fig. 3) showing some damage. In addition, there are numerous examples of isolated coenostea of corals and stromatoporoids preserved out of growth attitude within the mudstones and wackestones themselves; these cannot be recognized as being restricted to particular horizons because coenostea are too sparsely distributed and because the Upper Visby Beds have a somewhat nodular appearance where time lines are not easily delimited (see text-fig. 2). The consolidated limestone bands are frequently heavily bioturbated, burrows being readily recognizable but having indistinct walls. Burrows are up to 5 mm in diameter. Sharp-edged excavations in the sediment are rare.

Small reefs in the Upper Visby Beds are dominated primarily by stromatoporoids and to a lesser extent by tabulates. There are proportionately more tabulates than in the shallower water Höglint reefs. The stromatoporoids used in this study have been collected only from the level-bottom sediments of these beds and the reefs have not been studied. Collecting localities in the Upper Visby Beds are shown in text-fig. 1.

STROMATOPOROID MORPHOTYPES AND SPECIES

Stromatoporoids from the Upper Visby Beds are somewhat variable in growth form, ranging from laminar to domical although most are domical. The distinction between laminar and domical is arbitrarily based on whether the ratio of vertical height/basal diameter (V/B) is respectively less or greater than 0.1. Low, high, and extended domical forms are additionally recognized; the (arbitrary) ranges of these are shown in text-fig. 4A.

A small number of laminar and domical forms are approximately circular in plan view and are flat-based. These show no evidence of the effects of sedimentation or movement and appear to have grown undisturbed on a plane substrate to produce smooth enveloping forms of Kershaw and Riding (1978), symmetrical in median vertical section. Others are identical except that the basal surface is concave (Pl. 20), the concavity being due to growth on debris of skeletal organisms or hummocks of sediment as discussed by Kershaw (1980). The majority of specimens, however, as seen in Plate 20, contain some interdigitation of sediment at their margins (ragged margins). Usually this only slightly affects the overall shape to produce a series of small frills at the lower edges of what can be regarded as smooth forms since raggedness is hardly apparent on surface inspection. In many specimens, however, the raggedness is a major feature of the shape (Pl. 20). Stromatoporoids may also show displacement while alive (having continued to grow after displacement). These tended to develop rounded coenostea in which the distinction between upper and lower surfaces is difficult to make. Their constituent growth forms can therefore be seen only when sectioned. Also, even in specimens which are apparently single coenostea, sections show that many contain several stromatoporoid and coral coenostea of different species overgrowing each other.

Measurements on vertical rock faces (Kershaw 1979) show that stromatoporoids are low in abundance, ranging from none to twenty-eight (average nine) individuals per square metre representing 0–5% of the rock volume (average 1%, one-tenth of the value for the overlying shallower-water Höglint reefs). Very few stromatoporoids show signs of penecontemporaneous damage, reinforcing the impression that environmental energy was generally low, but some overturned specimens reflect intermittent disturbance. These stromatoporoids are small, basal diameters ranging from 20 to 250 mm with vertical heights from 2 to 70 mm although they can be

considerably larger (Mori 1970). Attitudes of coenostea reflect their stable convex-up shape in that 80% of the forms measured are preserved upright.

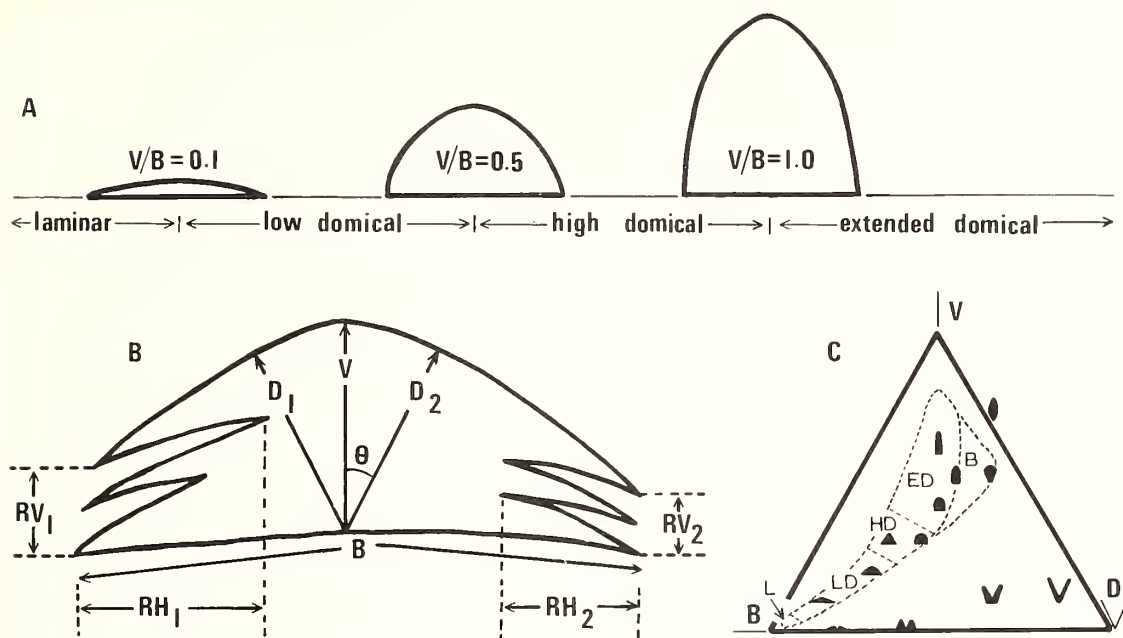
Other macrofossils are also low in abundance, particularly tabulate and heliolitid corals (often similar in gross morphology to stromatoporoids but can be more variable in growth form) which collectively occupy no more than a further 1% of rock volume. Low stromatoporoid abundance is also reflected in the low diversity stromatoporoid assemblage.

Nine stromatoporoid species have been reported from these beds (Mori 1969; Nestor 1979) but few of them occur commonly and only five were found in the sample used for this study. *Densastroma pexisum* Yavorsky is the most abundant, while *Pseudolabechia hesslandi* Mori, *Stromatopora impexa* Nestor, *Clathrodictyon simplex* Nestor, and *Clathrodictyon linmarssoni* Nicholson are much less common. All specimens of *C. linmarssoni* are incomplete and were not used in this analysis. Identifications are based on Mori's (1969) taxonomic work.

A range from laminar to high domical growth forms was found for all four species and suggests genotypic variability in all the stromatoporoids. *D. pexisum* formed 58% of the sample and so the environment must have been more suitable for its growth than for the other species. There is a temptation to suggest that *D. pexisum* is the dominant species, but since coenostea are generally isolated on bedding planes and the overall fossil content of these rocks is low (text-fig. 2), the idea of dominance for *D. pexisum* is inappropriate. Furthermore, there is no evidence of competition between stromatoporoids for space on topographic highs such as those created by the presence of dead stromatoporoids or other organisms.

Specimens were collected from all the localities in the Upper Visby outcrops shown in text-fig. 1, but only four of these were collected intensively. All specimens from these localities have been plotted on to the parameterization scheme of Kershaw and Riding (1978)—see text-fig. 5. The reader is referred to that paper for details of the triangular array; briefly, laminar forms plot in the bottom left-hand corner of the triangle and are increasingly domical towards the centre and top. Ragged specimens only are plotted in text-fig. 6. Text-fig. 4B illustrates the parameters used to plot data on to text-figs. 5 and 6. An amendment of the scheme allows an estimation of the amount of raggedness present in a specimen by measuring vertical raggedness (RV) and horizontal raggedness (RH) and then expressing them as ratios of V and B respectively (i.e. RH/B and RV/V). See Kershaw and Riding (1980) for details. Table 1A contains a summary of data on raggedness for the Upper Visby stromatoporoids. Text-fig. 4C shows the range of shapes generated by the array. Plate 20 shows examples of specimens containing several growth episodes; these could not be plotted as entire specimens because basal, vertical, and diagonal dimensions would be meaningless. Therefore it was necessary to treat each growth stage as an individual coenosteum with its own B, V, and D parameters and plot each separately in text-figs. 5 and 6. For example, Plate 20, fig. 5 contains two coenostea; Plate 20, fig. 7 contains three. In text-fig. 7 the distribution of basal diameters of all four species is illustrated; this is taken as a measure of coenosteal size. Although volume would be a more accurate estimate, it is not practicable to measure because two or more coenostea of the same or different species may form an inseparable composite and because of the variability of amount of sediment adhering to coenostea.

Chi-square analysis of the morphologies of the Upper Visby stromatoporoids reveals that *D. pexisum* is taller (higher V/B) than *C. simplex* and *P. hesslandi* at the 5% significance level and taller than *S. impexa* at the 7% level; this is regarded as sufficient for a significant difference to be accepted. *S. impexa*, *P. hesslandi*, and *C. simplex* display flatter distributions of shape, which are not significantly different from each other. The analysis involved only the non-ragged specimens, because ragged coenostea are exaggerated with respect to the vertical height which would give a false impression of the inherent shape of the coenosteum. Similar analysis of basal diameters demonstrates that *C. simplex* coenostea have significantly smaller diameters than those of the other species at the 0.1% significance level. The latter three species do not show a significant difference in basal diameters amongst themselves.



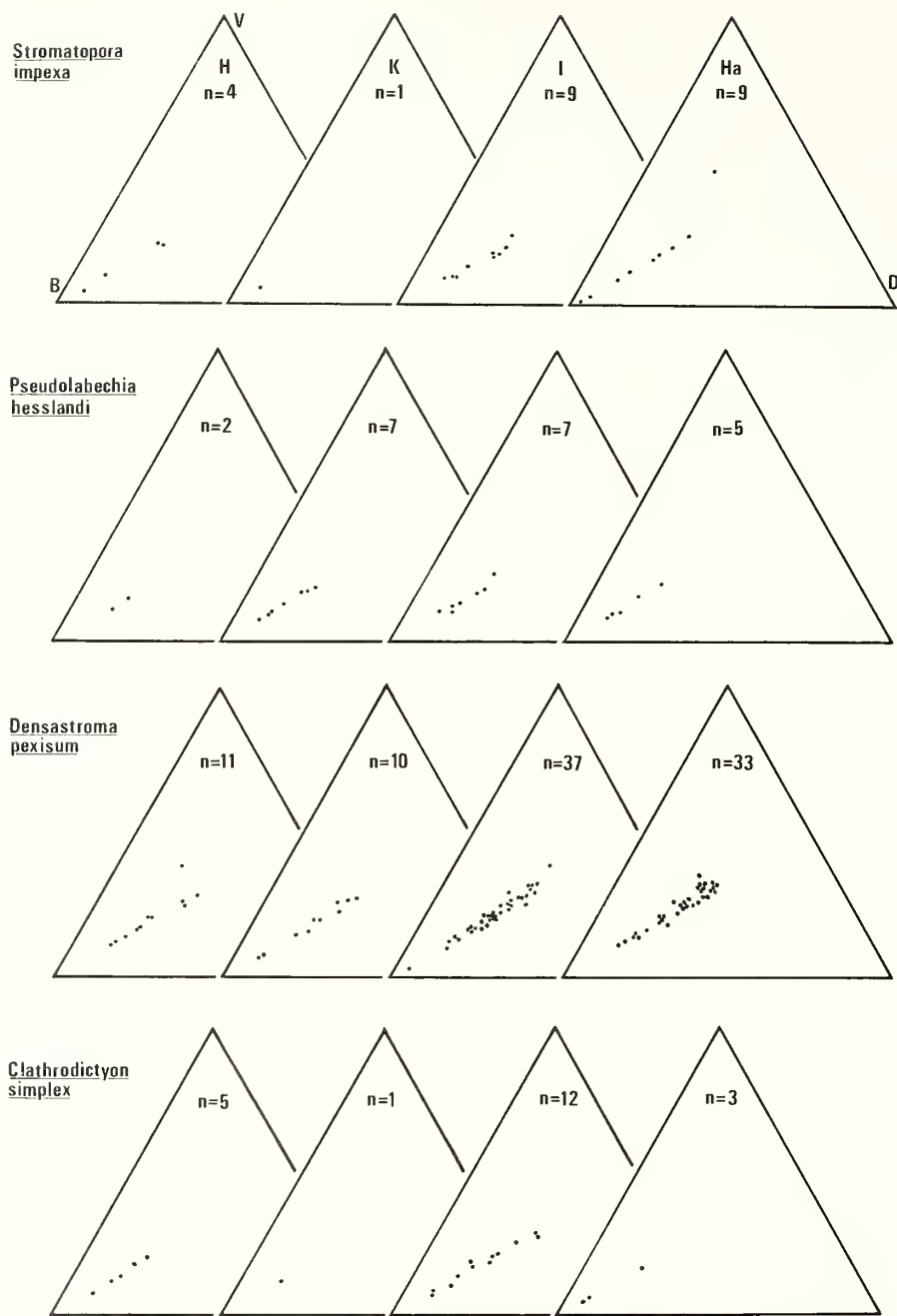
TEXT-FIG. 4. Shapes and parameters of stromatoporoid coenostea. A, terminology of stromatoporoid shapes used in this paper. V/B is the vertical/basal ratio. B, parameters measured for use in text-figs. 5, 6, 7 and Table 1A. V = vertical height, B = basal diameter, D (average of D_1 and D_2) = diagonal length at an angle (θ) of 25° from V . RV (average of RV_1 and RV_2) = vertical raggedness. RH (sum of RH_1 and RH_2) = horizontal raggedness. C, parameterization display of Kershaw and Riding (1978) showing examples of shapes generated by the scheme, the area occupied by stromatoporoids, and the approximate divisions of form. L, LD, HD, ED, and B are respectively: laminar, low, high, extended domical, and bulbous.

PATTERNS OF GROWTH

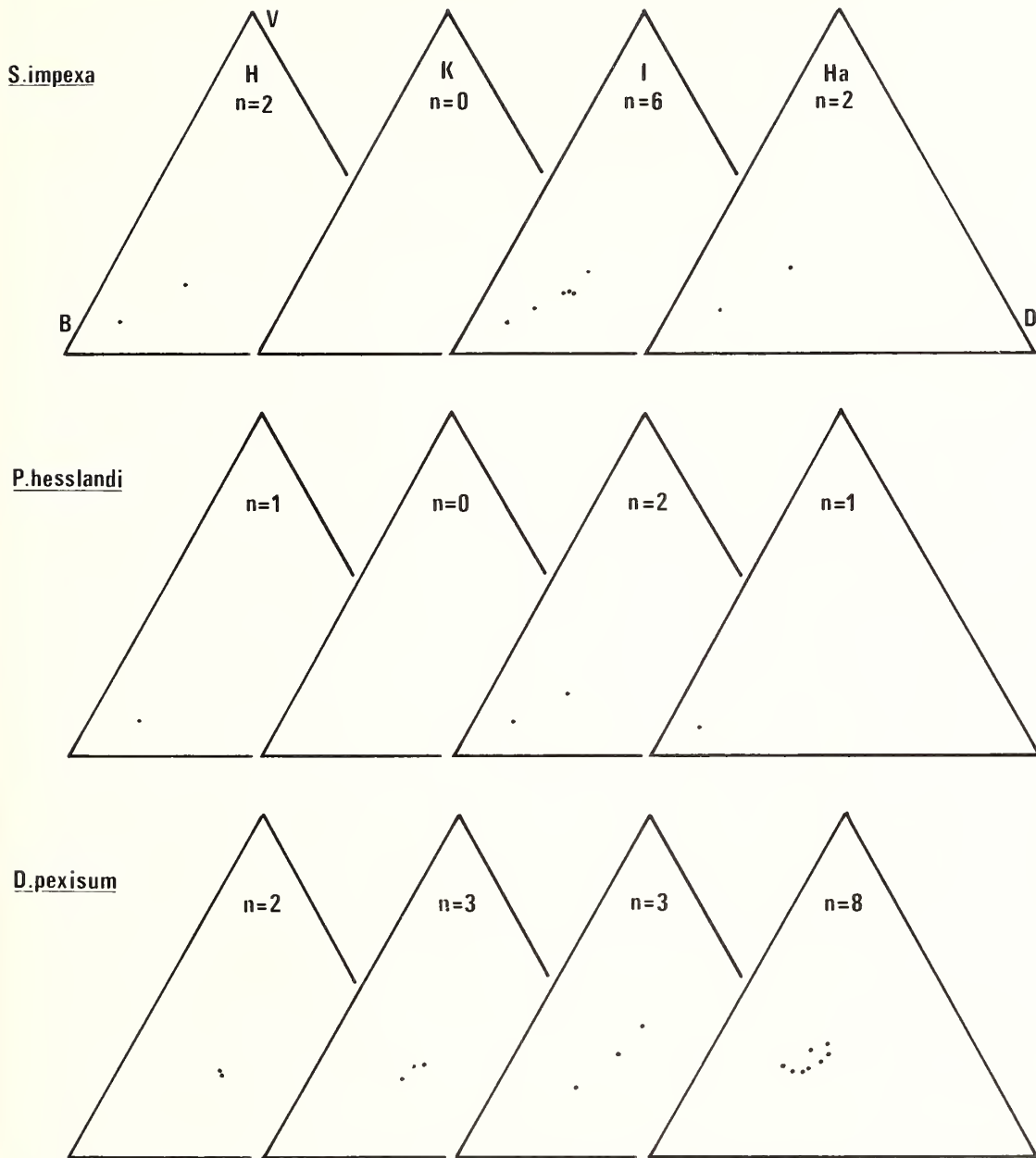
Stromatoporoids from the Upper Visby Beds, whether or not they have been affected by sedimentation or movement, do show a common style of growth in layers to produce laminar or domical coenostea; sedimentation and movement have merely disrupted that. Thus those specimens unaffected by these processes could be regarded as being the basic shapes of stromatoporoids from these beds. The basic shape is thus not a single form but a range of shapes from laminar through to high domical, each with smooth enveloping laminae (Kershaw and Riding 1978). Illustrations in Plate 20 show that sedimentation and movement had variable effects on the basic shapes of the Upper Visby stromatoporoids and although both processes may have operated on the same specimens, their effects can be considered separately.

Sedimentation

Several morphological features attributed to sediment choking are seen in the Upper Visby stromatoporoids. In smooth enveloping forms sedimentation has apparently not encroached upon coenostea during growth. However, while a lack of sediment interdigitations indicates that little or no sedimentation occurred up to the last-formed lamina (Pl. 20, fig. 1), cessation of growth at that point could be due to rapid sedimentation completely covering the growing surface. Such forms are uncommon; more usually in other individuals of the same species sediment is deposited on the marginal areas and although this is typically quite low in amount it can cover a large part of the coenosteal surface at any stage of growth (Pl. 20 figs. 2, 3, 6). Sediment forms discrete lenses and



TEXT-FIG. 5. Composite diagram showing morphology for each stromatoporoid species from the four main collecting localities, plotted on to the triangular display of Kershaw and Riding (1978). H, K, I, and Ha are, respectively, Höglint 2, Kneippbyn 3, Ireviken 3, and Häftingsklint 1.



TEXT-FIG. 6. Composite diagram showing triangular displays of morphotypes of ragged specimens only of each stromatoporoid species from the four main collecting sites. Note that text-fig. 5 includes these and the smooth forms. There are no ragged forms of *Clathrodictyon simplex* in the sample.

wedges which are indicative of intermittent deposition. The opposite view, that deposition was constant and growth episodic, is less likely because of the highly variable nature of sediment interdigitations in the stromatoporoids. Some have no such interdigitations (Pl. 20, fig. 1); others have a few large ones (see Kershaw and Riding 1978, fig. 2), while others have several small wedges in their margins (Pl. 20, fig. 2). Furthermore, any coenosteum may show a variety of thicknesses of sediment interdigitations and growth rates are unlikely to have varied to this degree in this fairly stable environment. However, stromatoporoid growth rates were almost certainly not constant since sediment deposition would presumably have caused a temporary reduction in growth rate. Stromatoporoid growth rate is poorly researched; the only really useful indicators are latilaminae—broad bands in coenostea thought by some to be akin to seasonal growth banding. However, great uncertainty surrounds the significance of latilaminae (Mori 1970) and they are not clearly defined in the Upper Visby stromatoporoids, except in *P. hesslandi*.

Movement

As with sedimentation events, a spectrum of movement effects is preserved in these specimens. Coenostea which have been moved would be expected to show damage at their edges, as in Plate 20, figs. 3 and 5. Domical coenostea, especially high domical forms, which have been overturned, have a high chance of being righted again quickly (Brenchley and Newall 1970; Abbott 1974) and in these cases it would not be possible to determine whether they had been overturned at all. Overturning is most clearly seen either where specimens are preserved in a non-upright position or where the direction of growth has changed. Note that the stromatoporoids are assumed to have grown upwards, approximately normal to the sediment surface in the Upper Visby Beds, which is the case in the majority of stromatoporoid assemblages. Specimens such as that shown in Plate 20, fig. 5 have been moved only once, others two or three times (Pl. 20, fig. 7), while others have a complex history of movement, often with sediment between the growth stages (Pl. 20, fig. 8). This sediment may have been deposited between growth stages, or, because it is rich in non-carbonate mud, adhered to stromatoporoid surfaces which touched the sea bed during movement. Stromatoporoid composites are common. Of 149 specimens, eighty-eight are single coenostea while fifty-one contain stromatoporoids which grew on, or were overgrown by, a number of organisms.

While some coenostea grew on (presumably dead) rugosans, gastropods, and orthocone nautiloids, others grew on heliolitids and tabulate corals, and the corals are also found overgrowing stromatoporoids. Table 1b shows the relationship between each species and its substrate and demonstrates that *P. hesslandi*, *S. impexa*, and *D. pexisum* are more common on mud, while *C. simplex* is more frequently found encrusting other organisms. A chi-square analysis shows that *C. simplex* is significantly more common on skeletal debris at the 1% level than the other three species. The latter show no difference amongst themselves. *P. hesslandi* and *S. impexa* show a similar distribution and together with *D. pexisum* had a greater tendency to grow on the muddy substrate.

Many of the stromatoporoid composites are monospecific and developed on continued growth from undamaged surfaces of overturned specimens. Others, with or without corals, appear to have built up as a consequence of the dead skeleton of one providing a stable surface for the next, slightly higher than the surrounding sea bed, from which sediment could be shed. As explained by Kershaw (1980), previous skeletons were almost certainly dead before overgrowth by later coenostea. Damage of coenostea in composites which have been overturned is minimal and consists of delicate marginal edges of coenostea having snapped off leaving sharply broken edges, frequently overgrown in later growth phases (Pl. 20, figs. 3, 5).

Internal lamination patterns

In addition to the variations of gross morphology and basal diameter, there are, in all species collected, differences in the arrangements of laminae within coenostea, which have a bearing on this discussion. Both laminar and domical forms can have enveloping laminae, giving the coenostea generally smooth outlines (text-fig. 8A, C; Pl. 20, fig. 1); most laminar forms are of this type. All but a few domical forms of all four species, while retaining a smooth outline, exhibit non-enveloping

laminae in the upper parts. Thus the lower parts started growth as laminar forms and became domical later on due to concentration of laminae in the central portion (text-fig. 8B; Pl. 1, figs. 2, 4, 5). Thus the overall pattern of development of laminae led to the same sort of smooth outline as individuals with fully enveloping laminae.

DISCUSSION

Sedimentation and movement effects preserved in the Upper Visby stromatoporoids may have been caused by a variety of processes and are considered in turn.

Sedimentation

Sediment settling from suspension may have produced the interdigitations seen in the stromatoporoids indicating intermittent sediment input. The Upper Visby Beds consist of alternating bands of mudstones and somewhat nodular limestones (text-figs. 2, 3) which may reflect regular, intermittent sedimentation events. Alternatively, sediment in stromatoporoid margins could have been deposited by transient currents. As mentioned earlier, there is no evidence of strong currents flowing across these beds but the presence of occasional debris bands suggest intermittent energy pulses, such as storm waves, stirring up the bottom currents, and redistributing sediment and benthic skeletal material. Such an interpretation is consistent with the view that the Upper Visby Beds represent a relatively deep water facies which would be only slightly affected by storm waves. Sediment in some interdigitations of the stromatoporoids contain coarse shell debris; others have fine-grained material only. Sediment may therefore have collected around stromatoporoid margins by both processes and in each case sediment settling on the higher parts of coenostea could have been easily shed on to the flanks. Thus laminar forms were more susceptible to choking by sedimentation than domical shapes, while the margins of all morphotypes in the Upper Visby Beds were prone to being smothered because of their subhorizontal aspect. That these delicate flanking areas of stromatoporoids grew in the first place indicates a low, if not zero, sedimentation rate most of the time. This is corroborated by three other lines of evidence: (a) the presence of (often abundant) encrusters on the undersides of upright stromatoporoids which appear to have grown in small cavities beneath coenostea; (b) the abundance of *Trypanites* domichnial borings in stromatoporoid upper surfaces (Kershaw 1980); and (c) considerable bioturbation of the sediment.

Movement

The agents causing overturning are unclear. Very small coenostea (e.g. where $B = 2$ or 3 cm) were conceivably overturned during bioturbation activity but since the bioturbation structures are rather small, larger coenostea would have needed more force to displace them. Orthocone nautiloids are present in the Upper Visby sediments and while alive may have predated on and dislodged stromatoporoids and corals from growth position, although there is a lack of the type of damage to coenosteal surfaces consistent with bite marks. The broken marginal edges of many larger coenostea suggest sudden movement of stromatoporoids consistent with displacement by storm activity as described above. Eddy currents produced by storm turbulence would have moved and overturned all coenostea below a certain size although the precise factors controlling movement of objects are complex and relate very much to local conditions as has been shown by models in flume experiments (Brenchley and Newall 1970; Abbott 1974; Kershaw 1979). These workers have shown that a combination of the following is involved: substrate composition and surface morphology, current velocity, and object size and shape. The responses of model stromatoporoids to a water current in a flume show that approximately equidimensional domical forms (where $V = B$) are the most stable of all, whereas laminar shapes tend to be flipped over by currents and tall domical forms which have a high centre of gravity are quite susceptible to overturning. Also, larger models are heavier and have higher competent velocities. These features would be expected to apply to the Upper Visby stromatoporoids. There is no evidence of attachment in the specimens studied and the assumption is that they grew on the unconsolidated sediment. Reef stromatoporoids, however, can be cemented to

TABLE 1. A, species totals and raggedness information for stromatoporoids from the Upper Visby Beds. R/S (ratio of numbers of ragged/smooth specimens), RV/V (ratio of vertical raggedness/vertical height), and RH/B (ratio of horizontal raggedness/basal diameter) are indices of raggedness. See text and Kershaw and Riding (1980) for explanation. B, relationship between the four stromatoporoid species and their substrates. The table was constructed by recording the substrate on which each coenosteum was found. 'other' includes the four species plus tabulate, heliolitid and rugose corals, gastropods, and orthocone nautiloids.

A

Species	Total	No. ragged	Mean R/S	Mean RH/B	Mean RV/V
<i>S. impexa</i>	23	10	0.43	0.63	0.51
<i>P. hesslandi</i>	21	4	0.19	0.59	0.36
<i>D. pexisum</i>	91	16	0.17	0.28	0.41
<i>C. simplex</i>	21	0	0.00	—	—

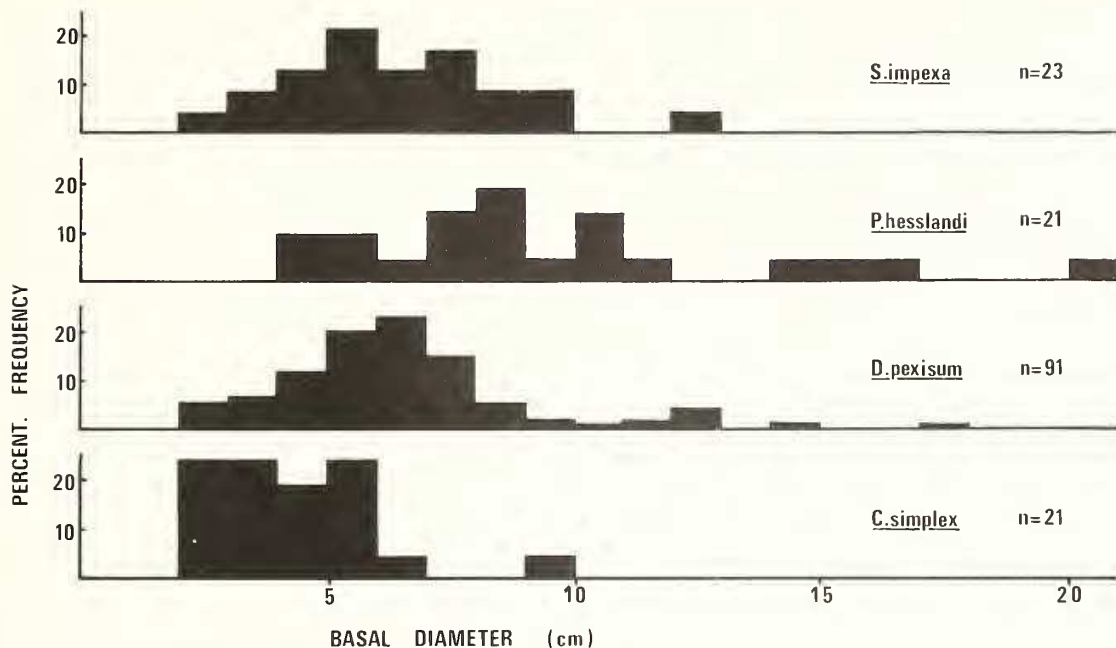
B

Substrate	Stromatoporoid species				
	<i>S. impexa</i>	<i>P. hesslandi</i>	<i>D. pexisum</i>	<i>C. simplex</i>	Total
Sediment	19	17	62	7	105
Other	4	4	34	17	59
Total	23	21	96	24	164

their substrate and may be in such close proximity to their neighbours that movement could be blocked in any case.

Competent velocity is also controlled by sediment type. On sand, low current velocities scour sediment from around objects and they can become buried as a result; at higher velocities a sandy substrate can facilitate coenosteal movement by creating a moving carpet of sand, reducing friction between stromatoporoid bases and the sediment. The Upper Visby Beds, however, are composed largely of mudstones and wackestones which provided a more coherent substrate than sand. Nevertheless, because bioturbation structures are not sharply defined, the sediment would not have been firm when bioturbated and probably, therefore, when colonized by stromatoporoids. Burial of objects by scouring of mud requires higher velocities than on sand because of the relatively lower mobility of muddy sediments. As a result, competent velocities are less on mud and once movement has started it is more easily perpetuated since the sediment is less yielding on impact. However, movement also depends upon substrate morphology. At water velocities just exceeding the competent velocity of a particular object, movement consists of a sliding motion across the sediment and may stop if an obstacle is encountered. At higher velocities an object may overturn when obstacles are reached and at even higher velocities overturning may occur regardless of presence of obstacles since the water is forced under the base of an object during its movement across the uneven substrate. The competent velocity of an object is increased if it is partially buried in the sediment because it has to be exhumed before movement can occur, and this necessarily involves some erosion of the substrate. Current surges, as would be expected during storms, can, however, produce eddies powerful enough to dislodge large objects which are unmovable by steady flow (Kershaw 1979).

The range of shapes and sizes of stromatoporoids in the Upper Visby Beds together with the unevenness of substrate must have given rise to a large variety of circumstances in the manner described above with respect to movement and overturning by turbulence. Also partial burial and variations of substrate composition played a part in determining the competent velocity for a given individual. Although it would be satisfying to have a series of values for competent velocities of the Upper Visby stromatoporoids, all these factors combine such that estimates for these particular



TEXT-FIG. 7. Size-frequency histograms of basal dimensions of each species.

coenostea are not very accurate; however, most coenostea would have been moved by velocities in the range 30–60 cm/s, based on experimental work with model stromatoporoids (Kershaw 1979).

Genotypic control on growth forms

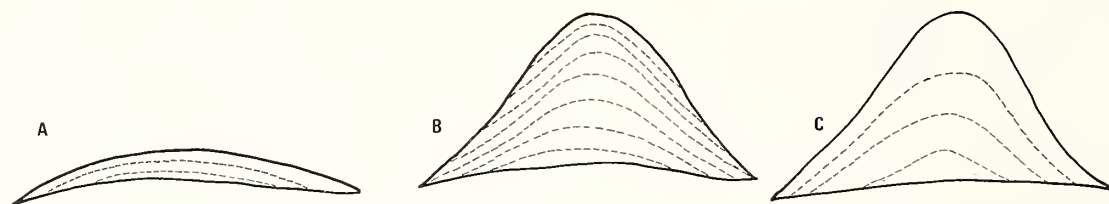
Recognition of the effects of sedimentation and movement and the consequent dismantling of composite specimens show up the true variations of coenosteal shape in the Upper Visby Beds (text-figs. 5, 6) and these in turn betray other processes at work. Each species shows a range of morphologies from laminar to high domical and suggest that under certain conditions laminar forms of a particular species developed, while under other conditions a domical shape was produced. A set of ecophenes therefore exists but the underlying controlling factors are not readily discernible. The shapes can be explained by a number of factors and these could include sediment-shedding capability, responses to current activity, variations in food, and oxygen supply. Variations in substrate consistency may also have affected shapes.

Stromatoporoids in the Upper Visby Beds do not show direct evidence of any of these possibilities but consideration of the sort of responses they might have made is worthwhile since little information is available on stromatoporoid palaeoecology.

A sediment-shedding capability is important for benthic organisms and developing a profile suitable for rejecting sediment landing on the growing surfaces is clearly desirable. Domical forms of all four species would have shed sediment from the apical areas, allowing growth to continue. Sediment interdigitations in stromatoporoid margins may well contain sediment shed from topographically higher parts of coenostea, and the stromatoporoids could clearly survive if the lower parts were smothered. If a domical growth style is a response to sedimentation then this suggests that sediment was continually settling on coenostea and would also suggest that laminar forms of any species grew in times (or areas) of little or no sedimentation. Unfortunately, the evidence of a low

sedimentation rate discussed earlier is compelling and laminar and domical forms do occur near each other on approximately the same horizons (text-fig. 2). The Upper Visby sea bed was probably uneven (Kershaw 1980) and a different interpretation is possible; a laminar form growing on a slightly raised area may have developed into a domical form had it settled as a larva in a lower area.

Differences in shape could have been a response to sedimentation, but could alternatively be due to a response to current activity for respiration and feeding. Although there is no evidence of strong current flow across the sediment surface, bottom currents must have been sufficiently aerated to allow the benthos to develop and this suggests the presence of at least gentle currents. Laminar organisms on a sediment surface in relatively deep environments live in water travelling slowly due to bed friction; the oxygen and food supply rates to them are consequently less than even a few centimetres higher up in the water column. The apices of domical organisms are not only higher in the water column, but because they interrupt the water flow they create eddies around them and keep the water well mixed in their vicinity. Since most stromatoporoids are domical in the Upper Visby Beds, they would have caused such local disruptions of water flow across the surface. It may be significant that tabulates and heliolitid corals also show a range of shapes from laminar to high domical which may be a response to the same stimuli.



TEXT-FIG. 8. Schematic vertical sections of stromatoporoid morphotypes from the Upper Visby Beds showing variations in the arrangements of laminae. See text for explanation.

Variation of substrate consistency is unlikely to have governed stromatoporoid morphology in these beds. Laminar forms would have been stable on an unconsolidated muddy substrate since coenosteal weight was low and evenly spread. Domical forms, with a higher mass per unit area of base, would have been better suited to firmer substrates. However, laminar forms are found not just on the substrate surface but also encrusted on skeletons of other organisms.

The four species do nevertheless show a different response to substrates. *C. simplex* is significantly more abundant as an encruster on the skeletons of other organisms than on the muddy substrate (Table 1B), suggesting a preference for harder and possibly topographically higher settling points. *D. pexisum*, *P. hesslandi*, and *S. impexa*, however, show a tendency to grow directly on the muddy substrate.

The pattern of accretion of laminae on the upper (growing) surfaces of these stromatoporoids described earlier may be indicative of shape-controlling factors. Significantly, laminae in upper parts of nearly all domical forms typically do not envelop earlier laminae completely. This feature may represent a mechanism by which growth was concentrated in the topographically higher central area of a coenosteum to cause local turbulence by interfering with water flow across the sediment and thereby feed more efficiently. By limiting growth to the central portion, metabolic energy would also have been saved if sedimentation affected the stromatoporoids since sediment clearly collected on and choked the topographically lower marginal areas. Whether this could be taken to imply that the presence of laminar and domical forms of the same species in these beds is due to variations of interplay between water flow and sediment deposition (from suspension) is open to conjecture, but the possibility nevertheless exists.

That *D. pexisum* is the most abundant of the four species studied could be explained by its generally taller profile than in the other three (text-figs. 5, 6). An upstanding shape is optimized for collecting food and oxygen and for shedding sediment, but also notable is that *D. pexisum* is generally less

ragged than *P. hesslandi* and *S. impexa* (Table 1) when horizontal raggedness is considered. The average value of RH/B of *D. pexisum* is lowest indicating that less of the upper surface area was covered by sediment in ragged forms. However, similarity of the RV/V values for the three species which have ragged forms means that, on average, the sediment wedges in *D. pexisum* are thicker due possibly to the steeper sides causing sediment to collect on a smaller marginal area than in flatter stromatoporoids. *D. pexisum* also has the smallest number of ragged forms of the three. No ragged forms of *C. simplex* were found in the sample. This species forms small coenostea (text-fig. 7). Its profile ranges from laminar to high domical but generally has a low profile (text-fig. 5); it may have been unable to thrive on the muddy sea floor. Its small size and lack of raggedness suggest a slow growth rate and a possible inability to shed sediment effectively; it may have been killed very easily by sedimentation.

The overall impression is that *D. pexisum* is the most abundant due to its height above substrate although the precise reasons as to why this should be so are as yet unclear.

CONCLUSIONS

This analysis of level-bottom stromatoporoids from the Upper Visby Beds on Gotland suggests that in a relatively poor, low diversity assemblage, different species developed alternative growth strategies and a variety of responses to the environmental pressures. Composite specimens reflect current activity across the surface of these sediments which resulted in overturning.

In a wider context, overturning and sedimentation are probably the two most important physical factors affecting the generation of stromatoporoid shapes and their effects have also been observed by the author in Ordovician and Silurian forms from Norway, Silurian forms from England and elsewhere on Gotland, and Devonian forms from England and Belgium in a variety of reef and non-reef environments. Most literature on stromatoporoid morphology also shows that these factors are common (e.g. Noble 1970; Kapp 1974; Cornet 1975). This study has documented the variety of their effects for a small assemblage and detailed examinations of these should be carried out elsewhere too.

An interesting parallel exists between the Upper Visby stromatoporoids and those from an almost identical environment in the Hemse Marls (Ludlow) in south-west Gotland. The most abundant species in the latter, *Pycnodictyon densum* (Mori 1970), has a similar internal structure to *D. pexisum* and is also usually low to high domical, also commonly with a smooth non-enveloping growth form. This could reflect the occupation of a similar ecological niche by two species at different times.

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